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Histology of the leaf of Taxodium. II.

STANLEY COULTER.

(WITH PLATE XI.)

II. The Mesophyll.—The parenchyma of the mesophyll consists of large, irregular, polyhedral cells, characterized by exceedingly thin walls and numerous infoldings. These infoldings are usually filiform, although in some instances they are somewhat thickened; in others, bifid; in others, terminated by a knob. Those cells nearest the epidermis and the fibro-vascular bundle have, as a rule, the more numerous and prominent infoldings. Scattered throughout this tissue are found the so-called "strengthening cells" (sclerenchymatous), either in groups or singly. They seem to be arranged according to definite plan, as in the foliage leaf of Pinus[10] and the fruit of the Umbelliferæ[11], but may be found in almost any part of the leaf. Sections from different leaves rarely show the same arrangement, and the same holds true of sections from different parts of the same leaf. They may, however, be expected in transverse section with a reasonable degree of certainty in two positions, (1) directly over the fibro-vascular bundle, immediately adjoining the epidermal cells of the outer surface of the leaf, and (2) near the ends of the leaf in its longer diameter. In the first case, they usually occur in groups of from 5–20, either massed or arranged in irregular rows, in which arrangement they often resemble a series of braces for the purpose of support (fig. 4). In the second case, they may appear singly, as a row stretching from the epidermal cells of the outer to those of the inner surface, or as a row running back from the apical cell, in or parallel to the line of the greater diameter of the leaf (fig. 5).

It rarely occurs that in this position these cells are more than three in number, or that they occur otherwise than in a straight line. It sometimes happens that these cells are entirely absent from this region (fig. 3), but this is not frequently the case.

Groups composed of from three to five cells, rarely more, are also found about midway between the epidermis and the fibro-vascular bundle, although these are sometimes wanting. It often happens that one-half of the leaf will be well supplied with these cells, while the other has only one or two,

[10] Coulter and Rose, BOTANICAL GAZETTE, xi. 258.
[11] Op. cit., xii. 239.

sometimes none. Although following closely no rule, they may roughly be said to occur, if at all, either in a hypodermal layer or layers immediately beneath the epidermis, or in a line about midway between the epidermis and bundle, but never, in either case, forming a continuous ring. In no case in the sections observed have they been found adjoining the bundle. It must be remarked, however, that they are not always found in the positions mentioned, but if present in relatively large numbers, the great proportion of them may be so referred. Apart from these general regions, single cells are found in almost every conceivable position, except adjoining the bundle. They are often found adjoining the respiratory cavities, more often in positions which indicate nothing concerning their function or their relationship to the other leaf tissues.

In transverse section they show the heavily thickened wall and present the peculiar appearance of "fullness," so marked in the case of this tissue in Pinus (figs. 3, 4 and 5).

In longitudinal section they are seen to be elongated prisms with pointed ends (fig. 10), and have the fibrous, banded appearance characteristic of these cells.

Comparing the development of this "strengthening apparatus" of Taxodium with that of Pinus, in which the location of these cells furnishes valuable diagnostic marks,[12] it appears to present the incipient stages of a system which in other sections of the same order becomes highly differentiated. In the imperfect annular arrangement of its strengthening tissue, Taxodium seems to be allied to Taxus on the one hand, and to Abies on the other, and in fact follows the prevailing rule that obtains in most leathery leaves.[13]

In Taxodium, the strengthening cells of the sclerenchymatous type do not surround the resin duct, or even necessarily appear in its region, its support apparently coming from collenchymatous cells, which here at least seem a transition form between the parenchyma and sclerenchyma.

In Pinus, on the contrary, the sclerenchymatous strengthening tissue seems to reach its highest development in its annular investment of the resin ducts, an investment which in Pinus sylvestris is in every instance complete and in some cases consists of two layers (cf. figs. 11, 12 and 13).

The strengthening apparatus of Taxodium distichum differs therefore from that of Pinus sylvestris in the following particulars: (1) In the absence of the continuous hypoder-

[12]Coulter and Rose, BOTANICAL GAZETTE, xi. 258.
[13]De Bary, Comp. Anat. of Phan. and Ferns, 419.

mal layer, which in Pinus seems collenchymatous rather than sclerenchymatous; (2) in the presence of this tissue in the median region between the epidermis and bundle; (3) in its absence at the resin duct; (4) in their indeterminate position.

In fact, so widely variant is the system in Taxodium itself, that it is only through an examination of some hundreds of sections that even an approximate disposition is to be found.

So far, therefore, as the strengthening apparatus is concerned, the leaf of Taxodium seems much less perfectly developed than that of Pinus.

Between the bundle and the epidermis of the lower leaf surface, relatively close to the latter, is found the single resin duct. The position is that to be expected from the nature of the leaf as shown by Thomas in Vergl. Anat. der Coniferenlaubblätter. No accessory passages are found in any other portion of the leaf. In transverse section the duct is seen to be somewhat irregular in outline, more nearly polyhedral than circular. The bounding cells, as above said, seem to be collenchymatous, and differ only in their thickening from the surrounding parenchyma. Those cells lying between the epidermis and the duct are the most heavily thickened, and by their arrangement furnish not only support but protection.

On the upper side of the duct the collenchymatous cells shade down gradually as to thickness of wall, until they reach the bundle. The duct thus seems to be perfectly supported and protected in the vertical line.

No marked extension of the thick-walled bounding cells is to be found laterally; they seem in that direction to pass somewhat abruptly into the typical parenchyma of the mesophyll (figs. 4 and 11).

The secretory cells of the duct, generally six in number, show in transverse section a marked difference in size and form. In size, they often differ as four or five to one, while their forms range from irregularly triangular, through narrowly elliptical to oval (fig. 11).

In median longitudinal section they are seen to have their longest diameter in the direction of the duct, while the bounding cells, which show numerous infoldings, have a relatively similar arrangement (fig. 10). The walls of the secretory cells are extremely thin and delicate, showing no thickening in any direction.

No tests were made to determine the nature of the con-

tents of the cells, and they are classed among the resin secreting cells because of their similarity in structure and arrangement to the typical resin ducts, and the close relationship of Taxodium to resin secreting plants.

The resin duct of Taxodium, when compared with the secretory system of Pinus sylvestris, appears remarkably rudimentary. Leaving out of view the greater number of ducts found in Pinus, a comparison of the duct of Taxodium with a single duct of Pinus confirms us in the thought that we have in the former the beginnings of a system, which is fully and strikingly developed in the latter. In Pinus we find in transverse section the almost perfectly circular outline of the duct, the sclerenchymatous investing ring at times of double thickness, the more numerous and regular secretory cells often of more than one layer, evidencing in every case a complete differentiation from the surrounding tissues, and an apparently perfected system.

In Taxodium, on the contrary, the whole duct gives evidence of an incomplete differentiation. It agrees more nearly in every particular with the duct of Pinus sylvestris as found at the commencement of its development in the young leaf (cf. figs. 11 and 12).

In this system, then, as well as in the cases of the stomata and the strengthening cell system, the leaf of Taxodium gives evidence of a much less complete development than that of Pinus.

III. Fibro-vascular system.—The fibro-vascular bundle[14] follows the general rule which obtains among the Coniferæ in having a separate course and free end, and also accords with the condition, so far as it has been investigated, among the Cupressineæ, in being single and median. While the bundle, which is of the collateral type, in transverse section, at first glance, seems to stand out sharply and distinctly, it is a matter of some difficulty to assign to it a definite limit, there being no bundle sheath and the parenchymatous elements of the surrounding tissues passing gradually into those which lie within the bundle itself. The orientation of the bundle is normal. Toward the end it is tapered somewhat, though not sharply. The xylem, which is irregularly semi-crescentic in shape, diminishes as it extends toward the upper leaf surface, until at its limit it consists of but two or three rows of tracheides. These, however, are in immediate contact with

[14] Geyler, Gefässbundelverlauf in d. Laubblattregion d. Coniferen, Pringsheim's Jahrb. VI., 55; Thomas, in Pringsheim's Jahrb. IV., 43; Cf. also, de Bary, Comp. Anat. of Phan. and Ferns, 300.

a series of heavily thickened cells, apparently collenchymatous, by which the bundle seems to be directly connected with the group of hypodermal sclerenchymatous cells heretofore described.

The xylem also diminishes laterally in the same manner, and is connected on either hand with an irregularly curved line of tracheides which project into the surrounding parenchyma. The line of the "fringe of tracheides," if,indeed,it can be called a fringe, can not be said to follow the contour of the leaf. In many cases it terminates abruptly, although in one or two instances in the sections made it was a prominent feature. Its presence, however, was not so constant, nor so marked, as might have been expected from the studies of Frank[15], and later those of Mohl[16]. In other respects the xylem seems in no wise different from that usually found in collateral bundles among gymnosperms.

The phloem, which shows regular rows of similar elements, in all the sections examined, seemed to have thicker walls than were to be expected in this section, but it is probable that the apparent thickness was due to swelling. In spite, however, of this somewhat unusual thickness of the membranes of the phloem, the boundaries between it and the xylem are sharp and distinct.

The phloem, as the xylem, diminishes somewhat laterally, and aids in giving the pointed appearance to the bundle in cross section.

As the xylem is connected by a series of thickened cells to the sclerenchymatous strengthening cells above it, so the phloem is connected with the resin duct by a number of rows of thick-walled cells, and thence by way of the collenchyma surrounding the duct, to that lying between the duct and the epidermis. In the vertical line from the phloem to the duct and thence to the lower leaf surface, the thickness of the cell walls seem unchanged, but in all other directions they diminish somewhat rapidly until they pass into the surrounding parenchyma. It is, as stated at the first, extremely difficult to say where the bundle ends, and the non-equivalent elements of the same form begin (figs. 4 and 2).

In longitudinal vertical section, the elements of the bundle present no marked features unless it be in the absence of spiral vessels, which were not detected in any of the sections made. I am not as yet prepared to say that they do not oc-

[15] Botan. Zeitung, 1864, p. 167.
[16] Ibid, 1870, p. 10.

cur, but they certainly are not so prominent or numerous as in Pinus and the other Coniferæ studied (fig. 10).

While the bundle is single and median, it has in some measure the appearance of having been formed by the coalescence of two bundles. If this be true, the coalescence occurs in the node, or immediately at the attachment of the leaf to the branch. Careful sectioning of the entire leaf failed to demonstrate the fact. In the work, I have as yet been unable to secure satisfactory sections either through the node, or through the exact base of the leaf. The point is therefore undetermined, with the probabilities, however, strongly against the view of the bundle being the result of a coalescence of two bundles.

The space occupied by the bundle, as compared with the other tissue systems making up the leaf structure, is smaller than is usually the case in conifers, much smaller than in Pinus sylvestris.

In comparing the fibro-vascular systems of Taxodium and Pinus, we find, as in the case of the other parts compared, a much less sharp differentiation from the non-equivalent surrounding elements, as well as a less complete development of the composing elements (cf. figs. 2 and 4 with fig. 13). It may therefore be safely concluded that, so far as leaf structure is concerned, Taxodium distichum presents a much less complete development and a much lessperfect differentiation of systems than is found in Pinus sylvestris. The facts in support of this view may be summarized thus:

1. In the less perfect mechanism of the stomata, evidenced by (a) the character of the guard cells, and (b) the slight modification of the subsidiary cells.

2. In the imperfect development and indefinite arrangement of the strengthening apparatus, shown by (a), the absence of the continuous hypodermal layer, (b) the absence of sclerenchyma from the region of the resin duct, and (c) the presence of single cells and groups of cells of this tissue, at indeterminal points in the mesophyll, referable to no theory of support.

3. In the presence of a single resin duct, showing (a) less regularity of form, (b) few and irregular secreting cells, and (c) imperfect differentiation from the surrounding tissues.

4. In the less complete differentiation of the bundle and the less perfect development of the elements composing it.

In all of these particulars, indeed, it more nearly resembles the conditions found in the young foliage leaf of Pinus

sylvestris than in the adult leaf. It may, therefore, be fairly regarded as showing the beginnings of a series of mechanisms and systems which in Pinus sylvestris have reached a high development. In Taxodium we find these variant in form, in position, in development; in Pinus, constant in all these particulars.

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EXPLANATION OF PLATE XI.—The magnification figures were upon the original drawings. These having been reduced one-half, the magnification figures must be correspondingly reduced.

Fig. 1. A. Single leaf of T. distichum in position. B. Leafy branchlet, with its crowded, 2-ranked, linear leaves.

Fig. 2. Cross section of leaf of T. distichum, showing the three regions of which the leaf is composed, distribution of strengthening cells, and position of resin duct.

Figs. 3, 4, and 5. Same, more highly magnified, showing also distribution of stomata. The three figures, as can be readily seen, are parts of the same section.

Fig. 6. Surface slice of T. distichum, showing irregular outlines of epidermal cells and depressed position of stomata.

Fig. 7. Section of stoma of T. distichum, showing depressed position, oval guard cells with heavily thickened outer walls, and large respiratory cavity.

Fig. 8. (Letter press, p. 80) Section of stoma of Pinus sylvestris.

Fig. 9. Longitudinal section, leaf of T. distichum, showing formation of apex of leaf by a continuation of epidermal cells of inner surface and modification of adjacent cells.

Fig. 10. Median vertical longitudinal section, leaf of T. distichum. *s*, superior surface; *i*, inferior surface; *st*, strengthening cells; *r*, resin duct.

Fig. 11. Resin duct of T. distichum, showing imperfect differentiation from surrounding tissues and irregular thin-walled secretory cells.

Fig. 12. Resin ducts of Pinus sylvestris.

Fig. 13. Transverse section of foliage leaf of Pinus sylvestris, showing the three leaf regions, distribution of strengthening cells and position of resin ducts.

BRIEFER ARTICLES.

A modification of the versatile anther.—In the genus Lilium, for example, it is a well-known fact that the anthers are at first erect, but as they mature the true versatile character becomes evident. An inspection of a young anther shows that the upper portion of the filament is slender, and inserted, or held in position, between the two lobes of the